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The Relationship Between Visual Sensor Equipment in Flying Insects and their Flight Performance – a 'Neurobio-Engineering' Approach

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14. ABSTRACT
The grant FA8655-09-1-3083, "The Relationship Between Visual Sensor Equipment in Flying Insects and their Flight Performance – a 'Neurobio-Engineering' Approach", that was awarded to support my research and the work of Dr. Sean Humbert, (UMD, FA9550-09-1-0075) has come to an end. In this final report on the scientific activities in my lab I will stay with the tradition to provide an overview of the work that is relevant to AFRL/AFOSR – which basically includes most, if not all projects undertaken in my lab during the funding period. Despite the fact that the seasonal availability of horseflies, robberflies and hoverflies did limit progress regarding a comprehensive comparative study of across several dipteran fly species, the following sections should demonstrate that we made some important advances regarding the biological design principles of multisensory reflex control. One of the major strategic moves was to focus on gaze stabilization as an approximation to study flight control. The rational being that head movements induced by multiple sensor systems compensate for unpredictable disturbances of the thorax flies encounter on the wing. In addition, Sean Humbert showed in his work that a head orientation which enables the alignment of head-centered sensor systems with the inertial vector significantly simplifies the measurement of state-changes required for feed-forward/feedback-based flight control. As a corollary of our joint studies we should state: Flying insects which are subject to significant inertial forces during flight and have limited computing power, gaze stabilization is a functional necessity that enables high aerial maneuverability. Because Sean Humbert has submitted a separate final report on his efforts, I will focus here on activities in my lab, adding occasional cross-references to his report where appropriate.

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"The Relationship Between Visual Sensor Equipment in Flying Insects and their Flight Performance – a 'Neurobio-Engineering' Approach"

(Period of finding: October 2009 – September 2013)

Final-Report

(16 March 2014)

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Contents:

1. General Summary of Achievements.

The grant FA8655-09-1-3083, “*The Relationship Between Visual Sensor Equipment in Flying Insects and their Flight Performance – a ‘Neurobio-Engineering’ Approach*“, that was awarded to support my research and the work of Dr. Sean Humbert, (UMD, FA9550-09-1-0075) has come to an end. In this final report on the scientific activities in my lab I will stay with the tradition to provide an overview of the work that is relevant to AFRL/AFOSR – which basically includes most, if not all projects undertaken in my lab during the funding period.

Despite the fact that the seasonal availability of horseflies, robberflies and hoverflies did limit progress regarding a comprehensive comparative study of across several dipteran fly species, the following sections should demonstrate that we made some important advances regarding the biological design principles of multisensory reflex control. One of the major strategic moves was to focus on gaze stabilization as an approximation to study flight control. The rational being that head movements induced by multiple sensor systems compensate for unpredictable disturbances of the thorax flies encounter on the wing. In addition, Sean Humbert showed in his work that a head orientation which enables the alignment of head-centred sensor systems with the inertial vector significantly simplifies the measurement of state-changes required for feedforward/feedback-based flight control. As a corollary of our joint studies we should state: Flying insects which are subject to significant inertial forces during flight and have limited computing power, gaze stabilization is a functional necessity that enables high aerial manoeuvrability.

Because Sean Humbert has submitted a separate final report on his efforts, I will focus here on activities in my lab, adding occasional cross-references to his report where appropriate.

1.1 Publications

During the funding period of this grant from Oct 2009 until the end of Sept 2013 my group has published 13 papers in peer reviewed journals (O32-45), 3 book chapter (R4-6), and 5 peer-reviewed conference papers (C4-9). Six of the peer-reviewed papers were published in high profile journals ranked ‘internationally competitive’.
Finally, I am a co-editor of last year’s proceedings of the ‘Living Machine Conference’ on biomimetic and biohybrid systems.
We are currently working four further scientific publications one of which will be submitted within the next week (O46), with the others to follow within the next month (O47-49).

1.2 Scientific Workshops, Conferences, and Seminars

In total I attended 22 scientific events within the duration of this grant across a wide range of subject areas from the five-yearly specialized International Conferences on Invertebrate Vision to the novel annual Living Machine Conference which is dedicated to bio-inspired technology. At three of those conferences Dr Kit Longden,

the RA on this grant, also presented his work. In addition I was invited to give seminar presentations in continental Europe and in the UK at 7 occasions.

Many of the conferences were in connection with the bio-MAV/UAS SOAR meetings, bio-inspired GNC at Eglin Air Force Base, or other events relevant to the Programme Arrangement between AFRL/AFOSR and DSTL on bio-inspired technology.

1.3 Poster and Oral Presentations at National and International Conferences

Members of my group presented 14 poster (A43-54) and oral contribution at 7 national and international conferences.

1.4 Funding

Current funding secured for research in my laboratory (excluding FA8655-09-1-3083):

- **Wellcome Trust** research grant, PI: *"Integrated reflex control" in Manduca.* [***Funding until end of April 2014***]

- **DSTL-sponsored EPSRC Industrial CASE PhD Studentship**, PI: *"The significance of (image) gaze stabilization - Comparative studies on gaze control design in flying insects using behavioural, computational, and electrophysiological techniques."* [***Funding until end of March 2015***]

- **DSTL National PhD Programme**, PI: *"The significance of (image) gaze stabilization - functional characterization of the neck motor system using electrical stimulation of identified neck muscles in blowflies."* [***Funding until end of September 2016***]

Grant proposals submitted:

- **AFOSR/EOARD**, PI, together with Dr Graham Taylor, PI, University of Oxford, UK, and Dr Sean Humbert, PI, University of Maryland: *"The mode sensing hypothesis"* [***1st year funding currently being set up at UMD***]

- **French-UK PhD studentship scheme (DSTL),** PI, together with Dr Stephane Viollet, CNRS, Marseille, FR: "Head-body movements in freely flying flies when chasing a dummy target"

Grant proposals in preparation:

- AFOSR/EOARD, PI, together with Prof Doekele Stavenga, University of Groningen, NL: "Polarization Vision in Horseflies"

1.5 Group size, Collaborations, and Scientific Impact

Group size:

2 RAs (postdocs), 3 postgraduate students (PhD), 1 MSc and 5 undergraduate students. I co-supervise a DSTL-funded DPhil student working in Graham Taylor's lab, University of Oxford, on the mode sensing hypothesis in *Manduca sexta*, and a PhD student in Barbara Webb's lab, University of Edinburgh, funded by the BBSRC who works on visual navigation in ants.

Collaborations:

I have collaborations at Imperial College in the Department of Bioengineering with: Dr Martyn Boutelle (Biosensors), Dr Simon Schultz (Neural Coding), Dr Manos Drakakis (Low-power VLSI technology), and Dr Reiko Tanaka (Compound Control). To study the functional anatomy of insects we still collaborate with the micro-CT group at the Natural History Museum, London. Our collaboration with scientists at the Paul Scherre Institute, Swiss Light Source, CH, to obtain high-resolution 4D data from tethered flying flies on the functional organization of their fight and neck motor systems is ongoing – we are currently publishing the results of to beam time grants I got awarded in the past. Collaborations with Prof Simon Laughlin (Cambridge) and Dr Graham Taylor (Oxford) have been maintained. Work with Graham Taylor and Prof Sean Humbert (UMD, USA) will be intensified by means of the AFOSR-funded grant on the 'mode sensing hypothesis'. A new collaboration has now been established with Prof Barbara Webb to study ant navigation. Further international Collaborations include work with Prof Martin Egelhaaf, Neurobiology, Bielefeld University, Germany; Prof Fabrizio Gabbiani, Baylor College of Medicine, USA; and Mr Ric Wehling at the AF Research Laboratory, Eglin, US. A new collaboration with Prof Doekele Stavenga, University of Groningen, NL, and Dr Stephane Viollet, CNRS, Marseille, FR are in planning.

Current Bibliometric Data and Scientific Impact:

Bibliometrics:

	March 2014
Number of citations*	2137
h-factor*	25

* = according to *"Google Scholar"*

Scientific Impact/Leadership:

- ***Reviewing manuscripts*** for more than 30 peer review journals, including *Nature*, *Science*, and *Neuron*.

- ***Reviewing grant applications*** for 10 funding agencies including *RCUK*, *NSF (USA), and AFOSR (USA).*

- ***Expert Reviewer*** for *European Commission FP7* collaborative project

- Member of ***Academic Editorial Board*** *of open access journal* **PLoS ONE**

- ***Financial Co-organizer*** AFOSR/DSTL "*Bio MAV SOAR*" meeting, Chilworth Manor, 2011, as well as UK follow-up meetings at Imperial College, London, and University of Oxford, 2012.

- Member of ***Programme Committee*** of Conference on *Biomimetic and Biohybrid Systems* "Living Machines", Barcelona and London 2012 and 2013

- ***Co-ordination*** of DSTL-supported virtual *Centre of Excellence* on Unmanned Autonomous Systems (*UAS – former "MAV"*)

- ***Local Co-organizer (Satellite events chair)*** of Conference on *Biomimetic and Biohybrid Systems "*Living Machines", London, 2013

- ***Co-applicant/proposer*** of research call initiatives in the area of sensing and actuation (ESF/NSF) and *"Robot Companions"*, Flagship proposal submitted to the European Commission.

I also took on leadership responsibility in fostering areas relevant to the remits of AFRL/AFOSR, contributing to high standards in scientific research by committing to reviewing and editorial work, as well as applying for an EPSRC Centre of Doctoral Training in *Bio-inspired Systems and Technologies*, strongly supported by DSTL.

2. Report on current projects:

I will outline the achievements during the funding period of this grant (FA8655-09-1-3083) in relation to the four major directions of my work:

2.1. ***Behavioural performance*** of multisensory motor control in dipteran flies
2.2. ***Biomechanics of motor systems*** involved in gaze and flight control
2.3. ***Neural mechanisms*** underlying multisensory motor control in dipteran flies
2.4. ***Modelling*** of multisensory motor control design

These four approaches result in a comprehensive description of sensorimotor control. The results obtained at different system levels and by applying a variety of experimental and theoretical approaches do inform and support each other. Altogether they enable an iterative cross-validation process that facilitates the derivation of models capturing the fundamental design principles of biological sensorimotor control.

Although funding for my research over the past nine years was also provided by the the BBSRC, Human Frontier Science Program Trust, Wellcome Trust, DSTL and Imperial College resources, I will briefly summarize earlier findings (presented in earlier reports) and the development over the last couple of months followed by a conclusion.

2.1. *Behavioural performance*

<u>2-degrees of freedom controller</u>

We applied a linear systems analysis approach to the gaze stabilization system in dipteran flies to quantify the interaction between the compound eyes (mediating optic flow information), the ocelli (mediating information on fast changes in attitude) and the mechanosensory halteres (mediating rotation rates) in the high dynamic input range.

In our original studies on *Calliphora* we performed a systems identification of the gaze stabilization system which showed a surprisingly linear performance under the conditions tested (C4). An intermodulation distortion (IMD) analysis indicated that internal non-linearities in the system contribute less than 4% to the output signal.

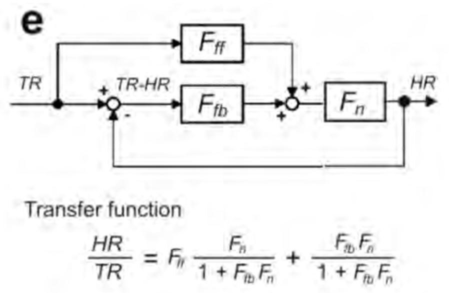


Figure 1: 2-degree of freedom controller combining feedforward signals provided by the halteres (F_{ff}) with feedback signals provided by the motion vision pathway (Ffb). The properties of the neck motor system are included by the transfer function of the neck motor system (Fn). For further details see text. Figure modified from (C4).

The resulting control architecture and transfer functions describing the relationship between the stimulus (thorax rotation, TR) and the systems output (head rotation, HR) are shown in Fig 1.

Recent work on the interpretation of the architecture and further analysis of the data revealed that the system including the halteres and the compound eyes can be described as a 2-degrees of freedom controller where 1 degree of freedom is given by a feed forward component (F_{ff}, halteres) and the second degree of freedom represents a feedback component (F_{fb}, compound eyes). This ingenious combination of fast feed forward signals mediated by the halteres and slow feedback signals from the compound eyes works as follows: immediate haltere-induced compensatory head roll shifts the retinal slip speed distribution caused by thorax rotation towards to lower dynamic range (subtraction of initial head roll from the thorax roll) that can then be analysed by the motion vision pathway of the compound eyes. Thus, the halteres ‘enable’ the visual system by eliminating those fast slip speed components the visual system would not be able to process due to its band-pass characteristics.

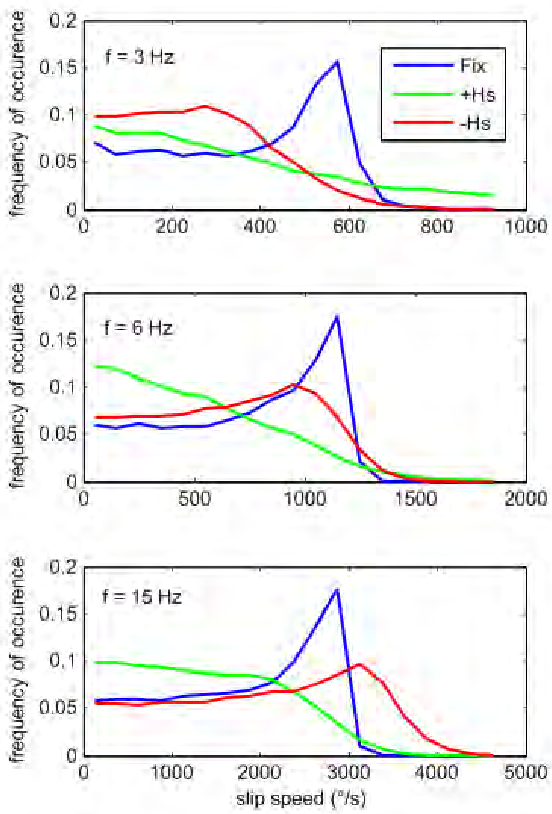


Figure 2: Probability density functions of retinal slip speeds under three experimental conditions and at three different thorax oscillations, 3 Hz (upper panel), 6 Hz (middle panel), and 15 Hz (bottom panel). The three traces in each panel show the distribution under condition where the head would be fixed to the thorax (HR = TR, blue), the halteres and the motion vision pathway (green), and only the motion vision pathway (red) contribute to compensatory head roll. Note that the contribution of the halteres to shift the slip speed probability density function depends on the stimulus frequency. At the highest stimulation frequency halter function is essential for enabling the processing of visual motion. If the halteres are disabled visual feedback causes a shift of the density function to higher slip speeds, which has a detrimental effect on gaze stabilization. (unpublished data).

The data presented in Figure 2 demonstrate the principle. They show probability density functions of the retinal image shifts (slip speed) the fly encounters during different experimental conditions, i.e. the frequency of occurrence plotted against slip speed. Three different oscillation frequencies of the thorax have been applied, 3 Hz, 6 Hz, and 15 Hz. The blue traces in the subpanels indicate the distribution the fly would experience if its head was was fixed to the thorax. The green traces correspond to the distribution when the head is free to move and both the compound eyes and the halteres are contributing to the compensatory head movements (+ Hs). In this case the slip speed distribution is shifted to the left, i.e. to lower slip speeds. Red traces show the shift of the distribution after the halteres were removed. At thorax oscillations of 15 Hz the significance of the feed forward component becomes most obvious (Fig 2, bottom panel). With haltere and compound eye contributions the slip speed distribution is markedly shifted to the left (green trace) while without halters (red trace) a shift of the distribution to the right is observed. These data demonstrate a co-operative effect of the two control degrees of freedom that is different from just adding up the signals generated by the compound eyes and the halteres alone.

This interpretation is in agreement with the qualitative finding that flies the halteres of which have been removed will immediately crash if thrown in the air. Only if a light weight thread is attached to their abdomen, they are able to fly again. The thread, in this case adds passive aerodynamic stability and dampens fast attitude changes resulting in high retinal slip speeds. With fast retinal slip speeds removed the visual system is sufficient to provide feedback signals for flight control.

A necessary condition for this 2-D controller to work is that the motion vision component of the controller provides stable feedback. We assessed the stability margins of the feedback controller and found that both the gain and the phase margins are unexpectedly high with 20 dB and 130 degrees, respectively. Our interpretation of those findings is that the system is specified to deal with a high variance of unpredictable input signals which, in combination with noise in the sensory pathways, potentially results in extreme output values without becoming instable.

We are currently writing up our work on the 2-degree of freedom controller for publication (O49).

Studies on gaze stabilization in robberflies

The supply of robberflies from the US turned out to be difficult. We observed a severe reduction of the life expectancy during intercontinental transportation by air, probably because the fly respiratory system does not tolerate the massive pressure changes in the cabin of air carriers. We therefore collected two UK robberfly species in the south of England, *Dysmachus trigonus* and *Philonicus albiceps*. The former species was used in preliminary electrophysiological experiments (see below), while the latter had been used for behavioural experiments to study gaze stabilization, applying the same linear systems approach as to blowflies the results of which were reported earlier.

Robberfies are more difficult to study under tethered flight conditions. They do not assume the same stable flight position a *Calliphora* and often extend their legs to counteract external body rotations. We were nonetheless able to perform some preliminary gaze stabilization experiments on *P. albiceps* which provided us with some insight regarding general principles and species-specific adaptations.

Figure 3 shows the data obtained from at least nine robberflies the thorax of which was oscillated over the range from 1-10Hz at an amplitude +/- 30°. The bode plots shown were obtained under four different conditions – the same that had been applies to blowflies in previous studies – in terms of sensory inputs: C1 (orange trace) all sensory inputs intact (n=11), C2 (dark blue) compound eyes and ocelli (n=9), C3 (red) compound eyes and halteres (n=11), and C4 (light blue) only compound eyes (n=9).

The most conspicuous difference in the gaze stabilization performance compared to the control condition where all sensors are intact was observed after the removal of the halteres; a similar result was found in blowflies (C4). Removing the halteres drastically increase the phase delay of the response (blue traces, bottom plot) – in particular when the ocellar input is disabled (light blue trace). The response gain shows no statistically significant differences, except for the condition where both the haltere and ocellar inputs are excluded. Any differences between the responses under the four conditions measured in the low dynamic range (1-3 Hz) are probably due to high interspecific variability. Overall, the results obtained in *P. albicepts* are comparable with those obtained in *Calliphora*. In both species haltere input reduces the phase delay of the response (orange and red traces, bottom plot).

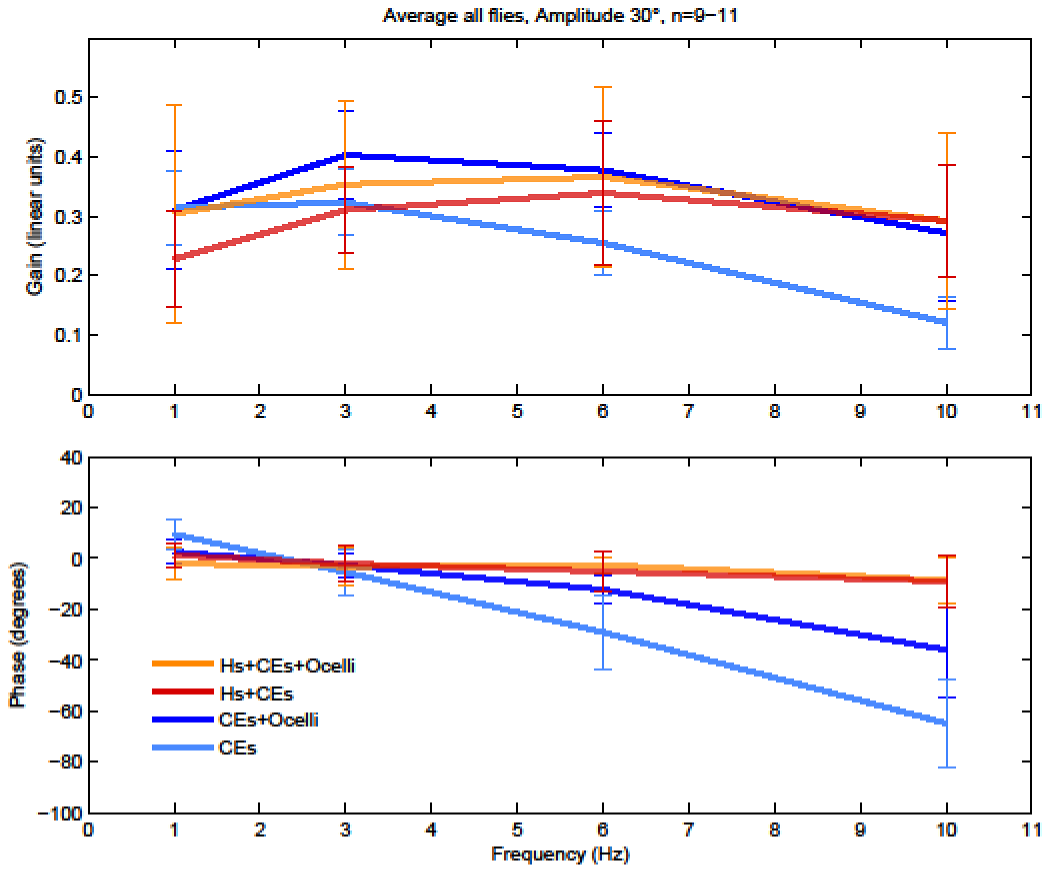


Figure 3: Frequency response of compensatory head roll in P. albiceps. Top plot: Head roll gain against oscillation frequency for four different combinations of sensory inputs (see inset, bottom plot). Probably due to a large response variability across animals no significant differences were found for three out of four conditions. When only motion vision contributes to the response the gain is significantly reduced for an oscillation frequency of 10 Hz. Bottom plot: The head roll phase angle relative to the phase of the stimulus as a function of stimulus frequency. Haltere contribution results in a minimal phase delay over the entire dynamic range tested. There is a significant difference in phase delay between responses obtained without halteres (blue traces) and all other stimulus conditions. The largest phase delay is observed when only the motion vision pathway contributes to compensatory head roll (light blue trace). (Unpublished data).

In a direct comparison between the gain of compensatory head movements measured in blowflies and robberflies mediated only by the motion vision pathway (ocelli covered and halteres removed) we found that compensatory head roll in *Philonicus* covers a higher dynamic input range compared to *Calliphora* (Figure 4). These results could suggest that the motion vision pathway in robberflies is tuned to higher angular velocities. But it could also mean that the neck motor system of the two species has different dynamic properties. The latter aspect would be supported by the fundamental difference the anatomical constraints of the neck motor. In robberflies the head is positioned more distantly from the thorax supporting larger head movements. Further functional anatomical (see below) and behavioural studies will be required before our results can be properly interpreted.

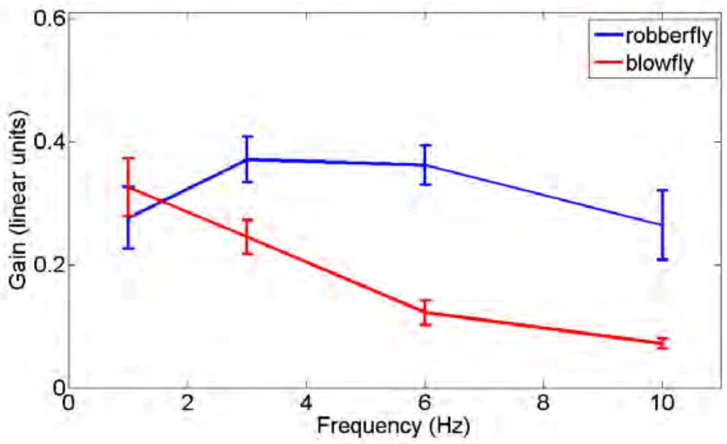


Figure 4: Gain of compensatory head roll in robberflies (n=9) and blowflies (n=7) mediated by the motion vision pathway. The thorax of the flies was oscillations at +/- 30° at different frequencies. At high stimulus frequencies robberflies show a significantly higher gain. Error bars give SEM (unpublished data).

<u>Interactions between motion vision pathway and ocelli</u>

Since the work by Parsons et al. (O20, O34) we know that the LPTCs (VS-cells) are modulated by ocellar stimulation suggesting both pathways to use a common sensory coordinate system, likely to be set up by the LPTCs (O26).

One of the major objectives of this project was to study the interaction between the compound eye-mediated motion vision pathway and the ocellar pathway in the gaze stabilization system of different dipteran species. Although the availability of species other than our lab-bred blowflies was rather limited throughout the duration of the grant, we did achieve comparative measurements on blowflies and robberflies.

In a first set of experiments we oscillated a dark visual hemisphere as a substitute for ground around tethered flying blowflies. Under these conditions the animals had access only to visual input, but no haltere information, where the ocelli were either covered (compound eyes) or uncovered (compound eyes + ocelli). The results in terms of compensatory head roll are shown in Figure 5. We found that under these two conditions, over the range of oscillation frequency from 1 – 10 Hz there was no significant difference between the response gain observed. The phase, however, showed a clear advance of the response when the ocelli were contributing for frequencies > 3 Hz. This result suggests a non-linear integration of ocellar and motion vision signals.

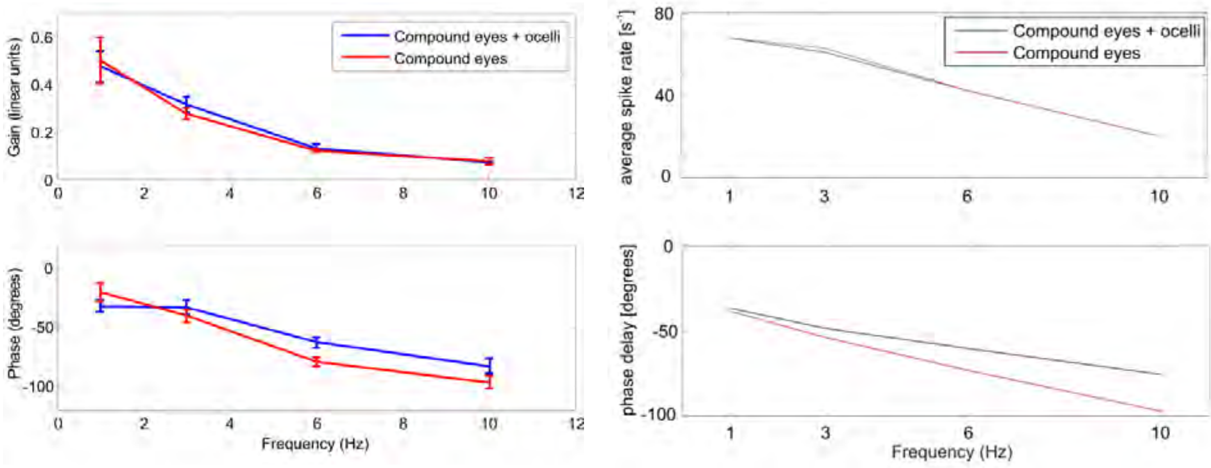


Figure 5: Compensatory head roll mediated by compound eye and compound eye + ocelli information. Left panels: Linear response gain (upper panel) and response phase (lower panel) plotted as a function of pattern oscillation frequency. Note that there is no significant difference between the condition with and without ocelli regarding the response gain while the response phase becomes larger for oscillation frequencies > 3 Hz. Right panels: The simulation of the ocelli and compound eye as simple highpass (tau = 12.5ms) and lowpass filters (tau = 12.5ms), respectively, combined with an 'integrate and fire model' of the descending neuron that included a static threshold non-linearity qualitatively captures the behavioural results. (unpublished results).

We combined a phenomenological approximation of the two sensor system properties by means of a low pass (motion vision) and a high pass (ocelli) filter, with time constants in the physiologically plausible range, and a biophysically motivated leaky integrate and fire model. A biophysically motivated 'integrate and fire model' was implemented to compute the membrane potential of a descending neuron that integrates the outputs from both sensor systems (Figure 6). Like all 'real' nerves cells the descending neuron incorporates a static threshold non-linearity. Only beyond a certain threshold membrane potential does the descending neuron generate action potentials, which are necessary to produce muscle contractions in the neck motor.

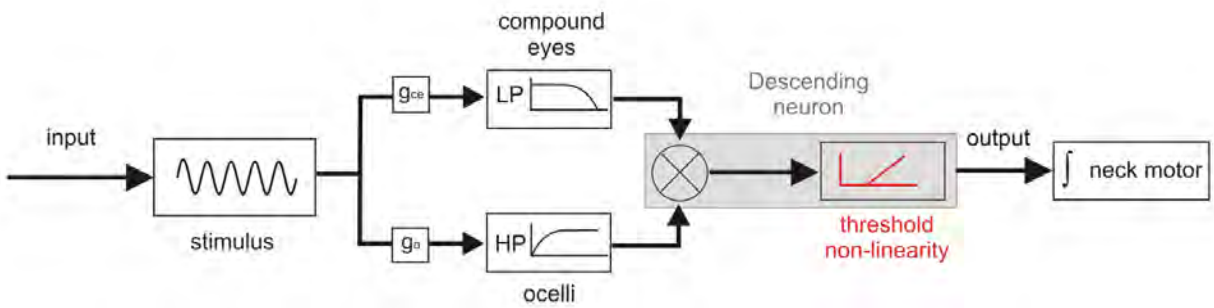


Figure 6: A model that qualitatively explains the observed phase increase in compensatory head roll of Calliphora when the ocelli are disabled while the gain stays the same for compound eye and compound eye + ocelli stimulation. (unpublished).

This model qualitatively reproduces the effect observed at the behavioural level: while the gain is the same for both experimental conditions, the phase of the responses at higher stimulus frequencies is advanced if the ocelli contribute (lower right panel). This comparatively simple model suggests a static threshold non-linearly as the potential basis for the observed behavioural data.

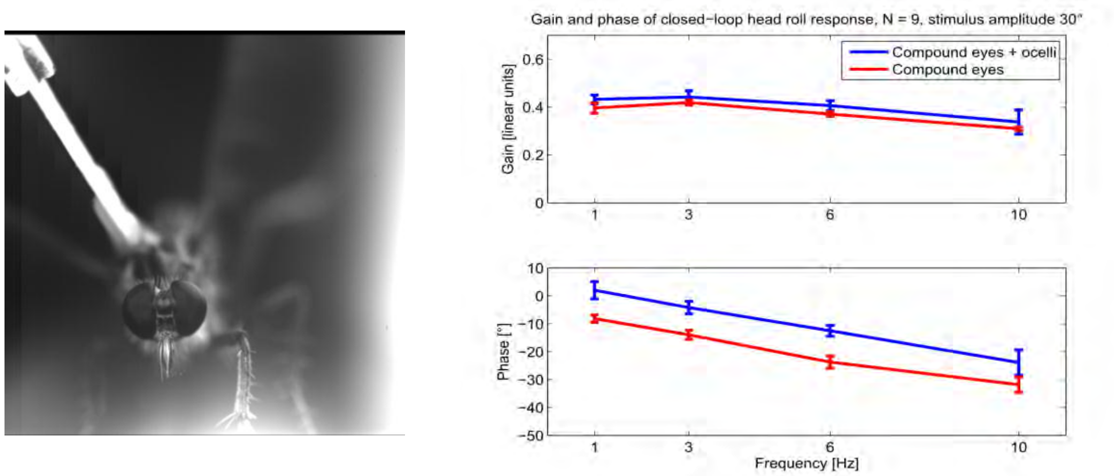


Figure 7: First studies on the interaction of ocelli and compound eye information in the robberfly Dysmachus trigonus (left panel). In these experiments the halteres of the fly were removed and rather than oscillating the ground pattern the thorax of the animals were sinusoidally rotated around the roll axis. The main senor systems contributing to the response were therefore the compound eyes or the compound eyes + ocelli. Right panels: Similar to the experiments in Calliphora, the gain was similar under the two conditions (upper plot) but there was a difference in the response phase (lower plot). (unpublished data).

We have also started performing specific experiments on ocellar and compound eye signal integration to study gaze stabilization in UK robberfly species *Philonicus albiceps* and *Dysmachus trigonus*. The behavioural results indicate that similar non-linearities as described for blowflies above may apply to the gaze stabilization systems in robberflies. Whether or not a static threshold non-linearity at the neuronal level best explains our findings regarding ocellar and compound eye signal integration across all dipteran species is not entirely clear at this point.

Next month we will perform more experiments on *Calliphora* – and as soon as they will emerge in the wild, on robberflies, horseflies and hoverflies – to substantiate our data base. We will also refine our open loop integration model. The model will be included as a first non-linear element in our otherwise linear closed-loop simulation platform of the gaze stabilization system (cf. section 2.4) before writing up the results for publication.

Altogether, the results of our behavioural experiments on gaze stabilization in dipteran flies proved to be a worthwhile paradigm to study the relationship between sensory and motor coordinate systems. We expect further advances regarding a quantitative description of the weighting given to the various sensor systems by applying band-limited white noise stimuli with different statistical properties and by new experiments where pattern and body rotations may be combined in different ways.

2.2. *Biomechanics of motor systems*

The neck motor system

A comprehensive understanding of the relationship between sensor and motor coordinate systems requires a functional characterization of the motor system. To this end we are combining functional anatomy based on x-ray techniques such as µ-CT with electrical muscle stimulations and biomechanical modelling.

Based on previous research in collaboration with the Natural History Museum London, we are currently advancing methods to increase tissue contrast in µ–CT scans to enable automatic segmentation of different tissue types. Our first results, still based on manual segmentation, provided us with a 3-dimensional reconstruction of the neck motor system in the blowfly *Calliphora* which will serve two purposes: (i) the 3D data allow us to refine our dissection methods in terms of minimizing structural damage to the system when placing electrodes for electrical muscle stimulation (ii) it will inform biomechanical models of the neck motor system, e.g. Finite Element Models, which capture the dynamic properties of the system.

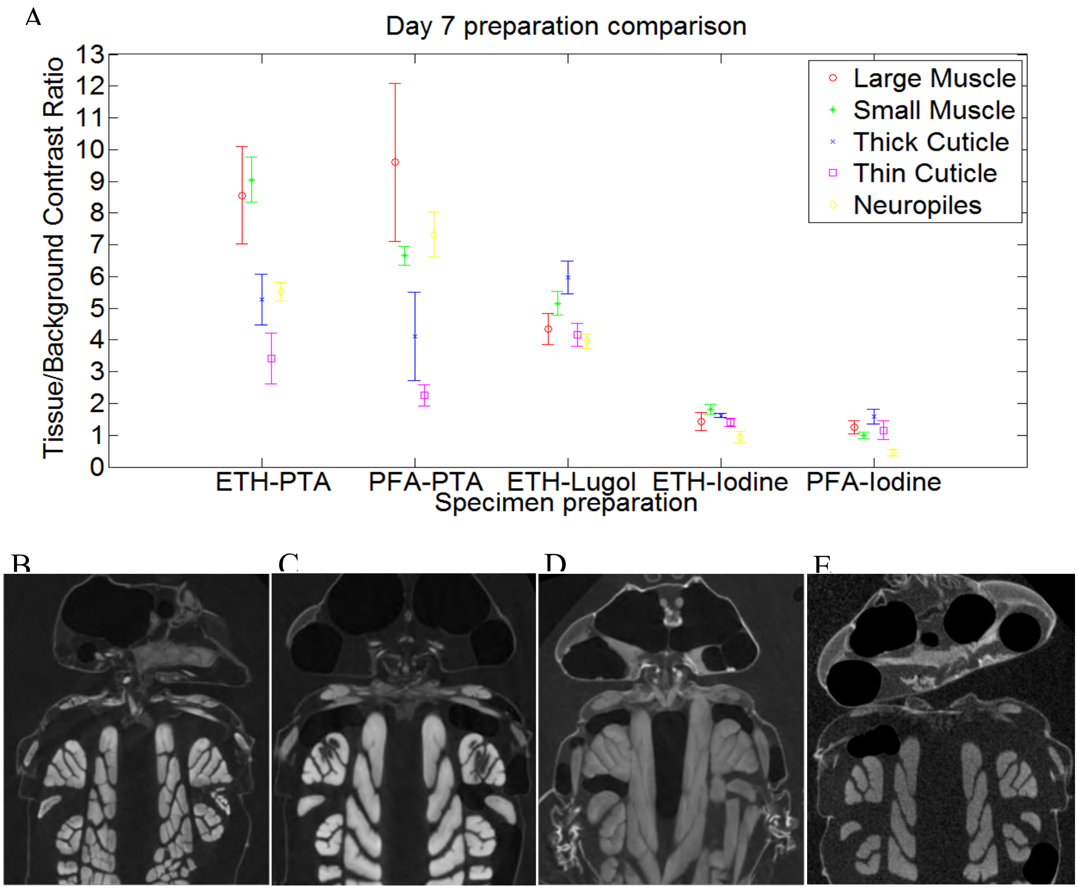


Figure 8: A quantitative and qualitative comparison of the 5 preparation methods for the final staining day. A: A comparison of day 7 contrast ratios across the 5 staining protocols, for tissue types (inset). B-E: Coronal slices of ETH-PTA (B), PFA-PTA (C), ETH-Lugol (D), PFA-Iodine (E) at approximately the same depth and orientation. The slice for ETH-Iodine exhibits similarly poor contrast to that of PFA-Iodine and is omitted. (data from O48)

Figure 8 shows some of the results we obtained in a study using different fixatives (e.g. ETH = 100 ethanol, PFA = paraform aldehyde) chemical agents (e.g. iodine, PTA = phosphotungstic acid) and staining protocols to increase the tissue contrast. In these experiments we did not optimize for the highest voxel resolution, which was just below 10 μm^3, but to increase the tissue contrast ratio. Our data show that the best ratios are obtained using a combination from ETH or PFA as a fixative and PTA as a contrast agent. We are currently preparing a manuscript for publication reporting the results on our systematic study to improve the µ-CT methodology (O48) for the functional analysis of insect motor systems.

In earlier work reported previously we applied iodine as a contrast agent to reconstruct the 3-dimensional organization of the neck motor system. As mentioned above, the results were meant to develop new dissection methods applied in the context of electrical stimulations of neck muscles to study their dynamic properties (Figure 9).

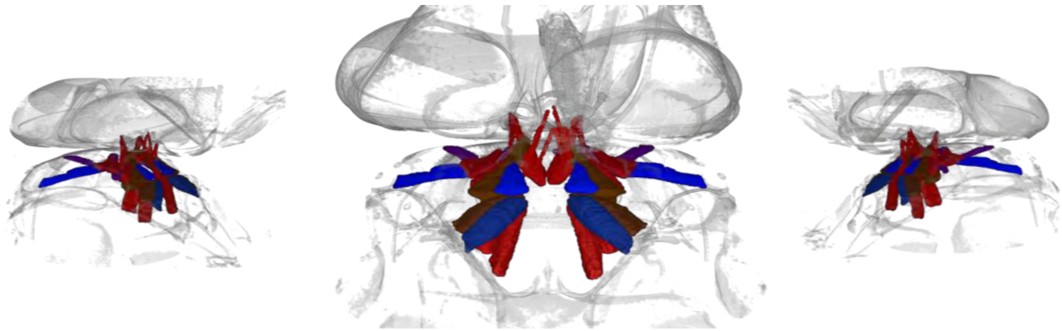


Figure 9: µ-CT-based reconstruction of the neck motor system in Calliphora. From left to right: right, top and left view of the blowfly head. False colours mark muscles attached to cuticular structures in the thorax and the head enabling gaze stabilization. (unpublished data).

The latest advances in tissue contrast presented above will allow us to refine the current 3-dimensional anatomical model of the *Calliphora* neck motor system. We are also planning to obtain similar data from other dipteran species for a comparative study.

A key component of our work will be the specification of a biomechanical model that captures the properties of the neck motor system. We decided to apply finite element modelling (FEM) to the system as it provides a convenient tool to describe and analyse the function of complex motor system. The FEM will be informed by our 3-dimensional anatomical data – and later by electrical stimulation experiments. Currently, we base the model on assumptions regarding the local Young's modulus. Despite this initial simplification of the system's functionality, we have been successful to generate head-body movements by introducing local forces simulating muscle contraction (Figure 10).

The combined approaches of physiological characterization and modelling of the system's properties will mutually support each other. Once a sufficiently detailed model is derived and validated, a dimensionality reduction will be performed to

obtain a simplified version of a neck motor system that may be implemented in technical applications.

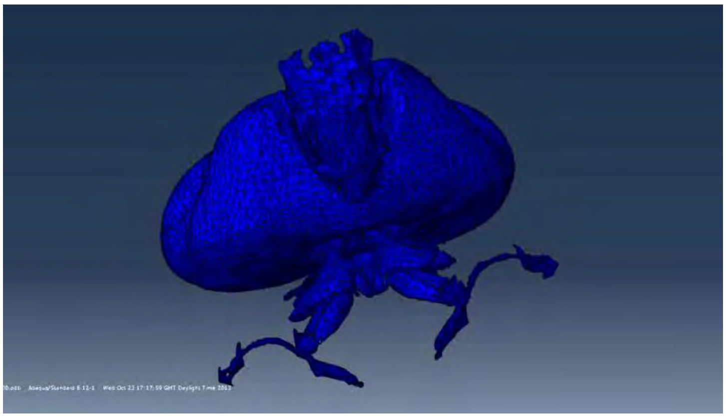


Figure 10: Finite model of the Calliphora neck motor system based on 3-dimensional anatomical data (ventral view). Each element describing part of a neck muscle is assigned a Young's modulus of a certain orientation. Simulating forces in the different muscles introduces relative movements between head and body. (unpublished data).

<u>The flight motor system</u>

Together with Graham Taylor's group in Oxford and a group of scientists at the Paul Scherrer Institut at the Swiss Light Source we have advanced x-ray scanning techniques in terms of spatial and temporal resolution in a way that enabled us to monitor the 4-dimensional operation of the flight motor in blowflies. The animals were subjected to hard x-ray radiation while being rotated around the roll axis in tethered flight. Under these conditions the flies were able to survive for several minutes and engaged on of showed asymmetric wing trajectories in an attempt to compensate for the externally forced rotation (Figure 11).

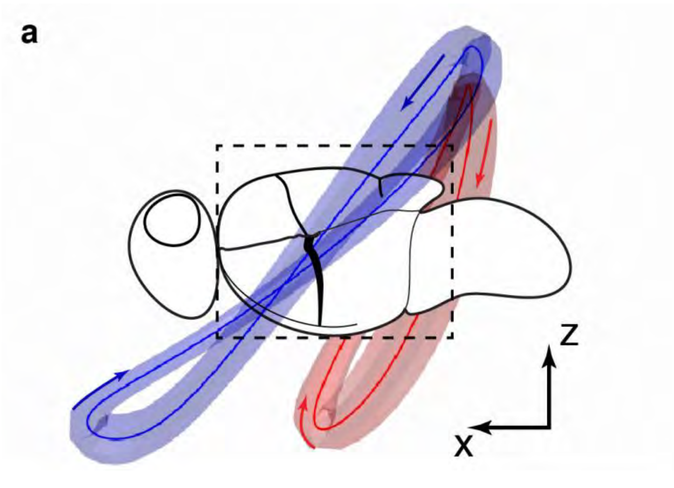


Figure 11: Schematic illustration of Calliphora observed in a synchrotron during tethered flight. The fly responds to a forced body rotation by generating a differential output of the flight motor - here by increasing and decreasing lift production in the left and right wing, respectively. The x- and z-axes correspond to the longitudinal and vertical body axes of the fly. (figure taken from O44).

Due to retrospective gating of images phase locked to the wing beat cycle we were able to observed the activity of the power and steering muscles during the compensatory flight manoeuvres. Figure 12 show an external view of the thorax and a view from the same perspective after virtually removing large parts of the cuticle. Phase contrast – as opposed to absorption contrast in µ-CT – was used successfully to

resolve even the buckling of tendons of steering muscles throughout the wing beat cycle.

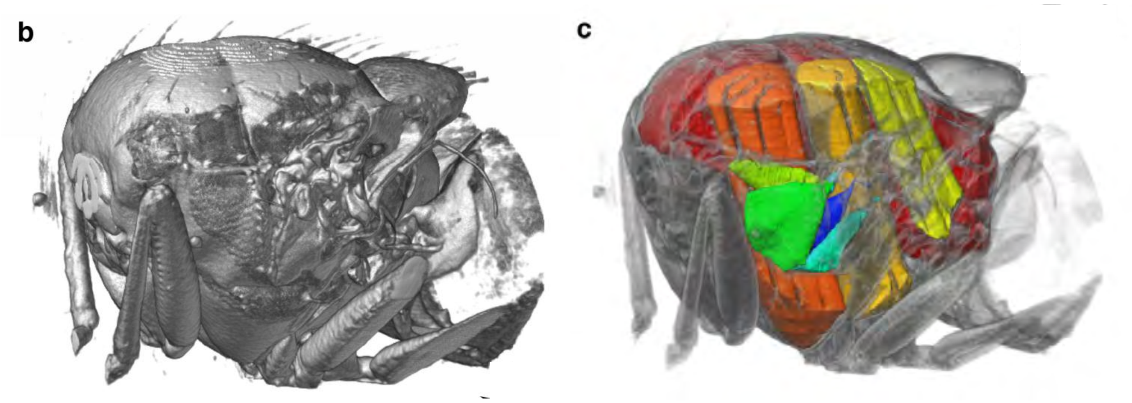


Figure 12: External and internal view of the Calliphora thorax. Left: External view of the thorax showing cuticular structures of the wing hinge and parts legs. Right: Virtual dissection of the thorax showing the power muscles of the flight motor (yellow, orange, and red) as well as four small identified steering muscles the activation of which could be analysed during asymmetric tethered flight in a synchrotron. (Figure from O44).

This technique allows us to analyses periodic movement patterns in any motor system of flying insects as long as an appropriate gating signal is available that is correlated with the movement. Given the high temporal and spatial resolution of the technique, in further studies we will be able to extract general principles of non-linear and linear operations in biological motor systems which will inform the development of bio-mechanical models. In combination with a better understanding of the neural mechanisms underlying these models will inform novel approaches to the design of small scale mechanical devices with strong potential for application in autonomous robotic systems.

On our highly successful synchrotron work, that was initiated by Daniel Schwyn, a former PhD student in the lab, we published two up-front reports in technical journals (O41 and O43) last year. A high profile publication of our results on the flight motor system is now accepted for publication in PLoS Biology (O44) with another one focusing on the ground-breaking new methodology currently being prepared (O46).

2.3. ***Neural mechanisms*** underlying multisensory motor control in dipteran flies

Optic flow processing depends on locomotor and nutritional state

A question of increasing interest concerns a notorious problem of biological systems that is even as significant for micro air vehicles with small payloads: limited energy supply.

Neural information processing is costly and requires sensory systems to adjust energy expenditure very tightly to the current needs. Work in our lab has shown that the activity of LPTCs in the motion vision system is increased during locomotion (O31, O36, O38).

In electrophysiological experiments where a tethered fly is able to walk on a trackball, by monitoring its forward speed and yaw rotations during stimulated with visual motion (Fig 13A, upper panel) we found that: The responses of the LPTC H2 (Fig 13A, lower panel) to temporal frequencies beyond 7 Hz of a moving patter are elevated when the fly is walking (Fig 13B, red trace) compared to those in stationary flies (Fig 13B, black trace). The increased responses are costly for the fly in terms of energy consumption but indicate a necessary adaptational mechanism to adjust its signalling range to a higher dynamic input range during locomotion. Food deprivation abolishes this adaptation in a gradual way (Fig 13C). We also found that the response increase was linearly related to walking speed in both fed (Fig 13D, grey line) and food-deprived flies (Fig 13D, black line), but that in food-deprived flies the increase was systematically reduced. In addition, the response increase was found to be inversely proportional to the number of days the flies were starved (Fig 13F). Our findings at the physiological level were corroborated by studying the yaw optomotor behaviour in flies, using wide-field motion for visual stimulation (Fig 13E, left panel). In fed flies the temporal frequency tuning of the bahaviour for frequencies from and above 4 Hz was high and stayed at a similar level over the entire dynamic input range (Fig13 E, grey trace filled circles). Flies starved for 3 days showed a significantly reduced optomotor response (Fig 13E, black trace) but recovered partly after 1 day of sucrose feeding (Fig 13E, grey trace filled triangles).

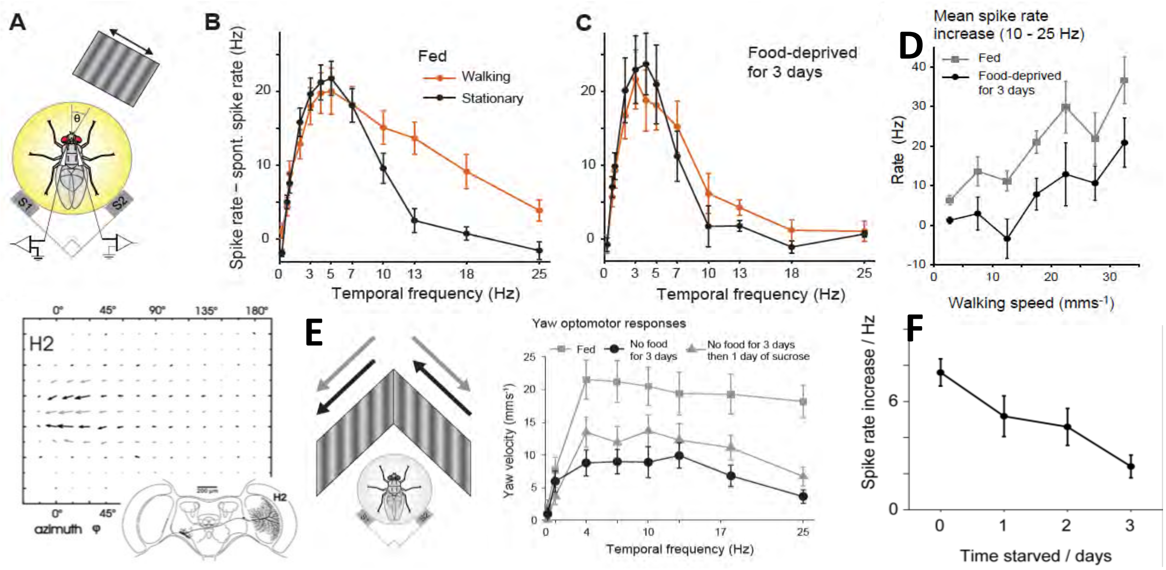


Figure 13: The temporal frequency tuning of the identified H2-cell depends on the locomotor state of Calliphora and its nutritional state. A: Schematic illustration of the experimental setup. B: Temporal frequency tuning in walking and stationary flies. C: Temporal frequency tuning in fed and food-deprived fies. D: Dependence of neural response on walking speed. E: Schematic illustration of optomotor setup (left) and optomotor responses in fed flies, food-deprived flies, and flies which were fed sucrose after 3 days of food deprivation. F: Neuronal response increment due to adaptation plotted over the number of days starved. Note that the walking-dependent adaptation of the temporal frequency tuning (panel B) is reduced due to starving. (Data from O45).

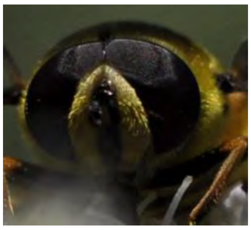
Together with other studies on the olfactory systems in starved flies, where the activity is actually increased (rather than decreased), our results suggest that under limited energy supply adaptational mechanisms in the visual system are reduced. The interpretation is that remaining energy resources are re-allocated to sensory task which increase the likelihood of survival – here: olfaction, which aids in locating food sources. This work has now been accepted for a high profile publication in Current Biology (O45).

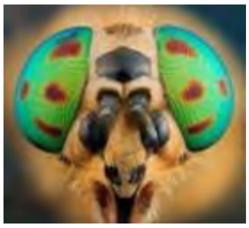
Comparative electrophysiology on Lobula Plate Tangential Cells in dipteran flies.

As mentioned earlier, to identify general principles and species-specific adaptations of multisensory integration and to relationship between sensory and motor coordinate systems supporting the 'Mode Sensing Hypothesis' (O42, R4) requires to study of a variety of different dipteran fly species. Ideally, those studies would include a description of the functional anatomy and modelling of the motor systems, behavioural experiments and an assessment of the neural populations involved in optic flow processing. The four families of dipteran flies we planned to include in our study are shown below. They all have different morphological and anatomical features likely to result in different aerodynamic properties, a pronounced variety of lobula plate tangential cells (LPTCs), and considerably different life styles. Together these aspects suggest specific relationships between sensory and motor coordinate systems.


Calliphoridae


Asilidae


Syrphidae


Tabanidae

Due to the limited availability of the different species, we have not yet been able to study LPTCs in all these species. Besides the detailed knowledge about the subpopulations of LPTCs in *Calliphora* – the reference species of this study – we were only able to record form a number of optic flow processing visual interneurons in robberflies so far, as I reported earlier. The results do far suggest that there are indeed species-specific differences in the response properties between *Calliphora* and the robberfly *Philonicus albiceps*. The responses of LPTCs, for instance, had a peak at higher temporal frequencies compared to *Calliphora*. We also found LPTCs in robberflies that had surprisingly small receptive fields, localized in the fronto-equatorial region of the visual field. Cells with such properties in *Calliphora* had not yet been reported although at the level of neck motor neurons (O26) similar visual receptive field sizes were found which potentially support some sort of edge-detection mechanism (e.g. Hengstenberg 1991).

Despite those some differences in the cellular equipment of the lobula plate, there is one type of LPTC that had been identified in *Calliphora* which was found in all other

species studied so far, even in the othopteran locust. A receptive field organization similar to that of the so-called H1-cell in *Calliphora* was also found in robberflies and horseflies (Figure 14).

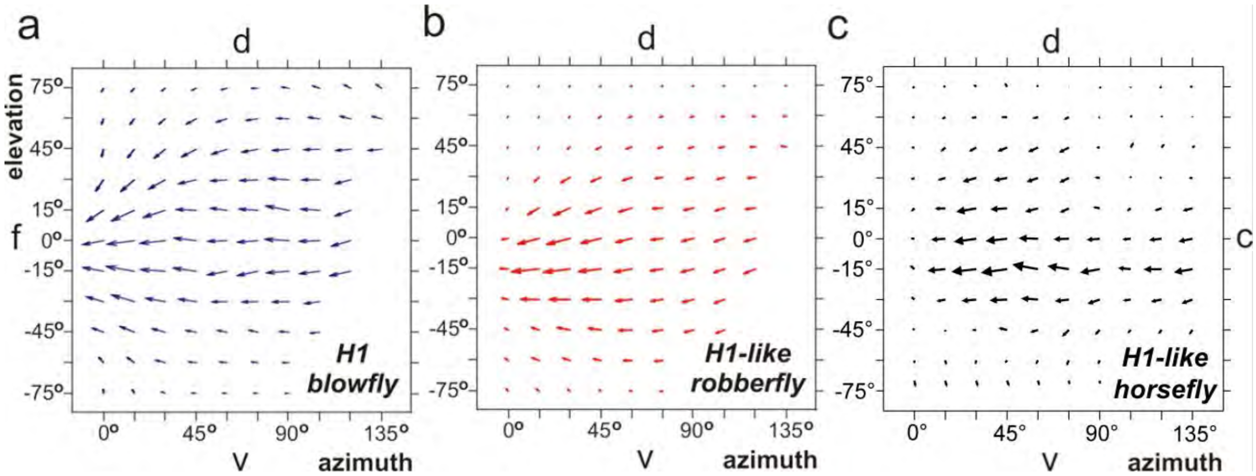


Figure 14: H1-like LPTCs in robberflies and horseflies. The panels show the directional motion preferences and sensitivities of motion sensitive interneurons in blowfly (a), robberfly (b), and horsefly (c) plotted against azimuth and elevation within the right visual field. LPTC of the type – which has been identified as H1-cell in blowfly – respond to back-to-front wide-field motion in the right visual hemisphere. In Calliphora the H1-cell in involved in detecting rotations round the vertical axis (yaw).

We will increase our efforts to investigate LPTCs in hoverflies, robberfies, and horseflies over the summer. A dedicated rig has been set up in the lab that allows us to perform both extracellular and intracellular recordings including intracellular staining to identify the cell under study. For flexible visual stimulation we will use LED panels as described in one of my earlier reports. In addition we will be able to use another rig that includes a back-projection system to enable wide-field optic flow stimulation.

<u>Fly-robot interface for studying multisensory integration</u>

A complementary approach to study multisensory integration has been developed over the last three years that utilizes a robotic fly-brain interface. As outlined in earlier reports the goal is to use neural spiking activity recorded on-board from an H1-cell to steer the robot under closed-loop conditions. To do so we had to miniaturize an entire electrophysiology set up so it fits onto a small 2-wheeled robot (Figure 15). This process has now been completed. Currently we are working on a control architecture that links the H1-cell signals to the motors driving the wheels. A challenge to overcome is that the the H1-cell increase its spike rate upon back-to-front motion (cf. Figure 14). Thus during forward motion of the robot the H1-cells in either side of the visual system would be inhibited and could not be used to control the wheels of the robot in order to avoid collisions with obstacles in the surroundings.

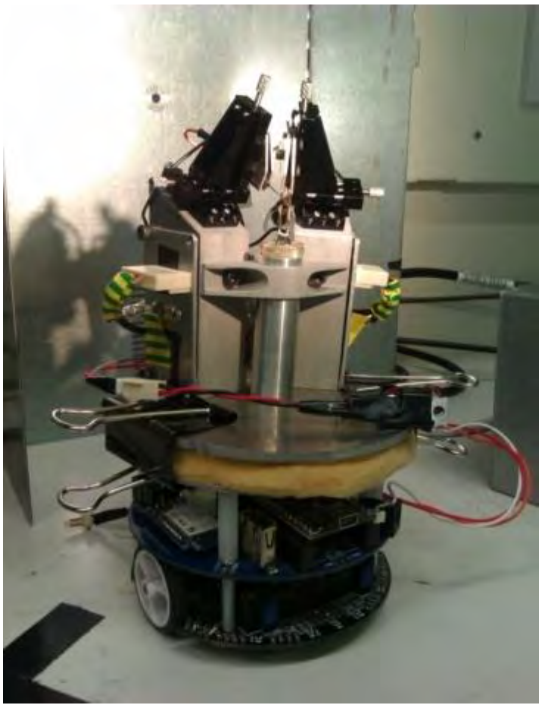


Figure 15: A robotic fly-brain-interface to study multisensory integration in Calliphora under closed-loop conditions. A small two-wheeled robot (diameter ~ 10 cm) carries a miniaturized electrophysiology setup. Micro electrodes will be positioned within the lobula plate using mini micromanipulators mounted on hollowed bases which contain shielded recording electronics. The recoding platform is isolated against the mechanical vibrations caused by the motors by a layer of foam material. The fly is fixed to a holder mounted on a central column. Signals from the H1-cell, a spiking LPTC, are extracellularly recorded and will be used to generate motor commands sent to the motors of the wheels. A/D conversion and signal processing will take place on-board. The neural signals will be used in a control architecture to avoids collision with obstacles in the environment while the robot is freely moving.

This problem will be solved by implementing a control architecture that exploits efference copies (forward models) of the command sent to the motors of the wheels forcing an undulating trajectory of the robot. The efference copie will result in a prediction of the neuronal response based on an internal model of the relationship between angular velocity of a visual pattern and the H1-cell response. The predicted spike rate will then be subtracted from the spike rate actually recorded from the H1-cell where the remaining difference is then used as a feedback signal to control the motors (Fig 16).

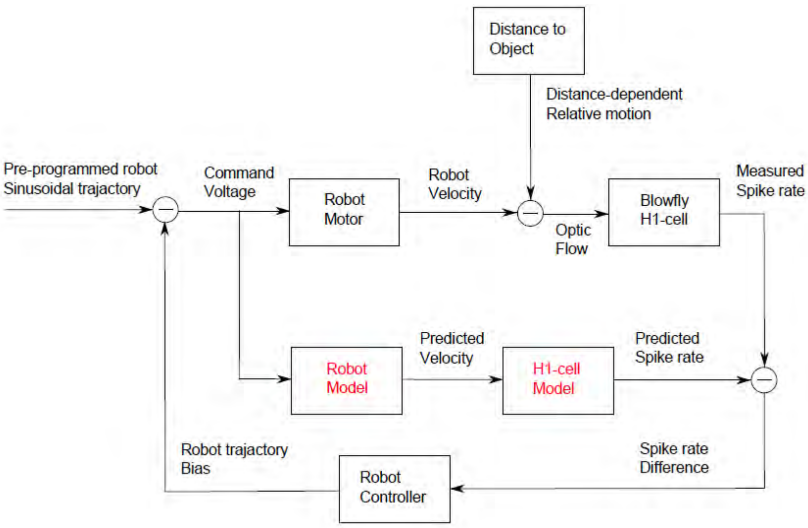


Figure 16: Control architecture to establish collision avoidance of a robot steered by a fly. 'Robot model' and 'H1-model' refer to the relationship between command voltage and angular velocity of the robot and the relationship between the angular velocity of visual motion and the spike rate of the H1-cell. (publication in preparation).

Such strategy requires (a) a forward model of H1-activity (Fig 17, left) and (b) the known input-output relationship between the control voltage sent to the wheels and the angular velocity of the robot (Fig 17, right). For the architecture to work in the

context of collision avoidance a certain response properties of the H1-cell are critical: close objects will introduce a stronger response in the neuron than objects at larger distances due to distance-dependent decreases in contrast. The other property is that the response of the H1-cell is a monotonic function of temporal frequency (Fig 17, left).

Work in of the group of Prof Egelhaaf on horizontal LPTCs suggested that so-called HS-cells may indeed be used by the fly to assess distance – although only during translational phases of flight following fast rotational body saccades. A similar strategy of ‘active vision’ in combination with an efference copy as described above will be implemented on the robot.

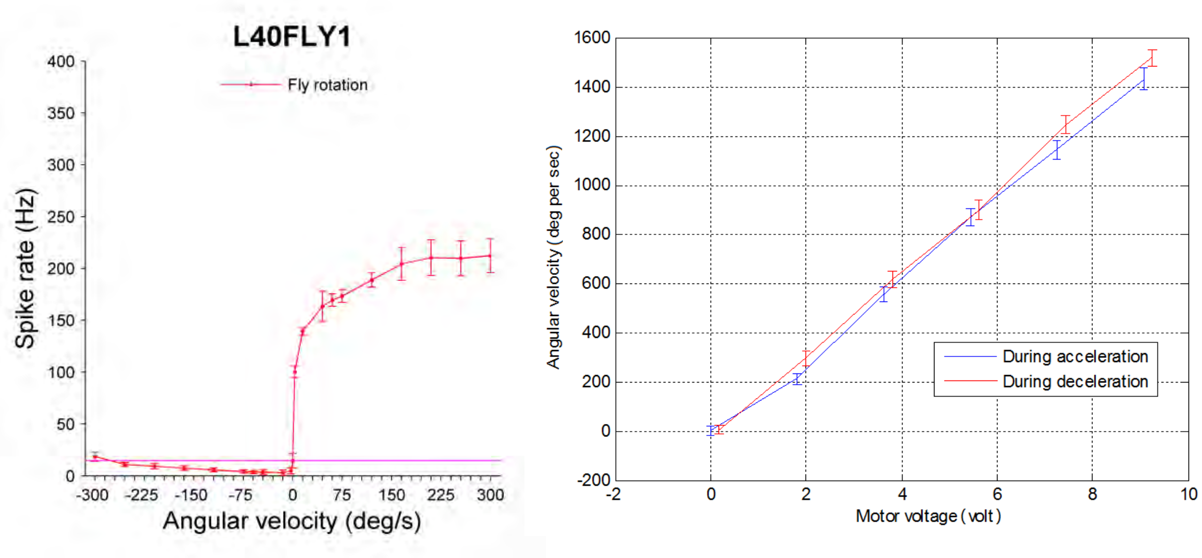


Figure 17: Angular velocity dependence of the H1-cell response in the lab environment (left). Note the monotonic relationship between positive angular velocities neuronal spike rate which will be implemented as ‘H1-cell model’ in the closed-loop control architecture in Fig 16. Right: Linear relationship between the command voltage and the angular velocity of the robot which will be implemented as the ‘robot model’ in the closed-loop control architecture shown in Fig 16. (publication in preparations).

Eventually, we will simultaneously record the activity of other LPTCs of which we know they reflect the integration from sensory modalities other than motion vision (e.g. O20, O34) in a fly that is actually moving in space. We will then compare the neuronal responses recorded when different senor systems are disabled to assess signal integration under closed loop conditions.

2.4 Modelling of gaze stabilization

In collaboration with Dr Reiko Tanaka (Dept Bioengineering) we have been working continuously on refinements of a closed-loop simulation platform that models the gaze stabilization system of *Calliphora*. Most modelling approaches were based on behavioural experiments (section 2.1) and assumed – in a first approximation – a linear time-invariant system (e.g. C4). One major result of this approach was the 2 degree of freedom controller discussed above.

We have recently expanded the concept of the 2 degree of freedom controller to include the stabilization of the body against unpredictable external disturbances. It is important to mention that the diagram shown in Figure 18 is purely conceptual at this point in time and has not yet been tested experimentally with respect to the flight control component. What makes it plausible in terms of its potential implementation in the fly nervous system is that the same pathways known to control the animal's gaze are also thought to be involved in flight control. The core functionality of the flight control system is therefore likely to also dependent on the 2 degrees of freedom controller that has been described earlier.

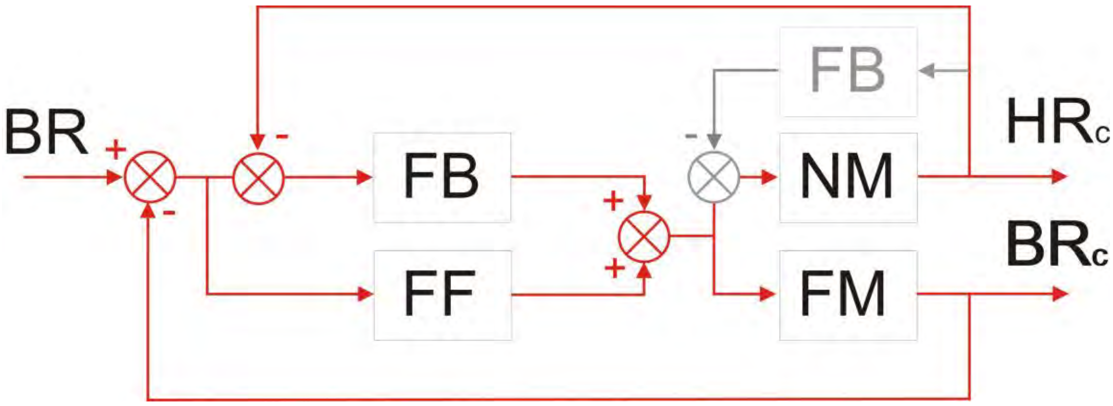


Figure 18: Control of gaze and flight by a 2 degrees of freedom controller. Upon externally caused body rotations, a fast feedforward (FF) signal initiates both, compensatory head movements (HR_c) by activation of the neck motor (NM) system and compensatory body rotations (BR_c) through the action of the flight motor (FM). This fast response mediated by the haltere system reduces the retinal slip speed and thus enables the processing of optic flow along the slow motion vision pathway generating a feedback signal (FB) that contributes to both, HR_c and BR_c. Any remaining misalignment between the head and the body may be measured by the prosternal and chordotonal organs providing slow feedback signals (FB, grey) primarily to the neck motor system. (unpublished work in progress).

The control diagram in Figure 18 only considers inner-loop reflexes induced by external perturbations. During voluntary movements of body to change the trajectory, motor commands are sent to both the neck and the flight motor, and efference copies may be sent to the sensors supporting the feedforward and the feedback degrees of freedom so that the sensory signal generated as a result of voluntary action does not immediately cause a counteracting stabilization reflex. Similar schemes in spirit have been proposed earlier (R3) and Chan et al 1998. But firstly, they did not include a 2 degree of freedom controller. And secondly, they are only weakly supported by experimental evidence. Further closed-loop simulations including the scheme will

have to show (i) its viability and (ii) may inform the design of further experimental studies in its support or to falsify it.

In a recent study that has been accepted for publication at a control engineering conference we took a very different approach: We propose a novel mathematical framework based on an extended Kalman filter and a controller with infinite-horizon dynamics that minimises the costs associated with muscle contraction on the one hand side and imperfect gaze stabilization on the other (C9). In closed-loop simulations the model explicitly considers inherent constraints in biological systems, i.e. ambiguity and noisiness of sensor signals, inevitable response delays along sensory pathways, and limited energy supply for both the neck motor and the nervous system. Figure 19 shows the block diagram of the system.

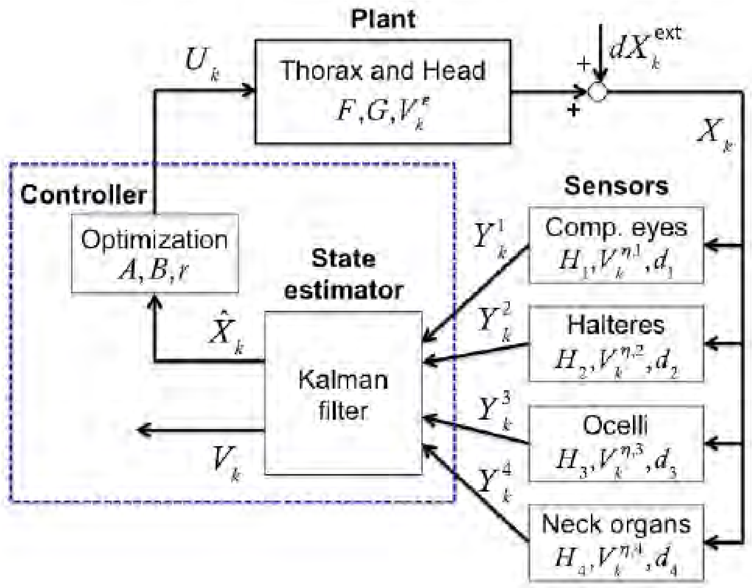


Figure 19: Gaze stabilization system based on a Kalman filter-type state estimator and a controller providing optimized sensoy feedback to the motor plant. The scheme involved the motion vision pathway provided by the compound eyes, halteres, ocelli and neck proprioceptors which measure external disturbances, dX_k^{ext}. Small deviations of from a horizontal head orientation are tolerated due to the cost associated with muscle contraction. (from C9)

Although it is unlikely that flies have evolved an implementation of an optimized Kalman filter in their nervous system the proposed framework may as well be of interests for technical applications including autonomous micro air vehicles.

3. Conclusion:

Within the period of funding we have made significant progress in all areas of research carried out in my lab and on the basis of collaborations. The collaboration with Sean Humbert turned out to be very successful with us meeting at least once or twice a year, being in regular email contract and talking on the phone whenever some immediate discussion on our collaborative work was required. We published together on 3 occasions and are still working together on a first paper where the modes of motion in *Calliphora* are related to the preferred rotation axes of its VS-cell in addition to another conference publication on a bioinspired ocellar sensor.
We also engaged on another grant proposal to AFOSR/EOARD together with Graham Taylor on the 'Mode Sensing Hypothesis' which is a key element of the implementation road map of the AFRL-DSTL programme arrangement on bio-inspired technologies. The start of the grant had been significantly delayed due to the financial situation in the US. Meanwhile funding for the first year has been set up at the University of Maryland.
One aspect regarding the scientific programme of this grant that had been underestimated was the impact of limited availability of dipteran species which cannot be bred in the lab. Although we developed strategies to acquire other species by means of wild catches and temporary breeding of hoverflies except for *Calliphora* we were quite often short of experimental animals. This was, however, compensated for by many complementary approaches and alternative aspects sensorimotor research so that a constant stream of high profile output was produced in my lab during the funding period.
Another limiting factor certainly is a comparatively small size of my research group. I mentioned in my previous reports already that the comprehensive approach I apply to insect sensorimotor control at four different system levels and across several species would definitely benefit from a group size twice as large as my own. This, however, would require me to write way more grant applications with I would like to do, but cannot because of a limited time budget.
In an ideal scientific world and to facilitate research along the merits of AFRL and AFOSR stronger support in terms of finances would be much appreciated. Having said this, it is very clear that I would not have been able to engage on a more comprehensive approach on sensimotor control without the continuous funding stream provided by AFRL/AFOSR – normally through EOARD.

Irrespective the limitations mentioned so far, we have made excellent progress in particular with work on the 3- and 4-dimensional functional characterization of the neck and flight motor systems, work that was initiated originally by Daniel Schwyn and Martina Wicklein in my group. The work on state-dependent processing which is highly relevant to the topic of energy efficient information processing was also initiated in my lab by Kit Longden and has developed into an aspect several world-leading labs are now working on. And finally, the quantitative behavioural work and modelling projects in my lab and in collaboration with others scientists has reached a continuous level of comparatively high productivity.

Holger G Krapp London, 16 March 2014

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Diploma Thesis:

Krapp H.: Ein Verfahren zur schnellen Bestimmung der lokalen Vorzugsrichtung und Bewegungsempfindlichkeit im rezeptiven Feld von visuellen Interneuronen der Schmeißfliege *Calliphora erythrocephala*. Diplomarbeit. Eberhard-Karls-Universität Tübingen 1992.

PhD Thesis:

Krapp H.: Repräsentation von Eigenbewegungen der Schmeißfliege *Calliphora erythrocephala* in VS-Neuronen des dritten visuellen Neuropils. Dissertation, Eberhard-Karls-Universität, Tübingen, 1995.

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O1. **Krapp H.G.** and Hengstenberg R.: Estimation of self-motion by optic flow processing in single visual interneurons. *Nature*, **384**: 463-466, (1996)

O2. **Krapp H.G.** and Hengstenberg R.: A fast stimulus procedure for determining local receptive-field properties of motion-sensitive visual interneurons. *Vision Research*, **37**: 225-234, (1997)

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O17. **Krapp H.G.** and Gabbiani F.: Spatial distribution of inputs and local receptive field properties of a wide-field, looming sensitive neuron. *Journal of Neurophysiology*, **93**: 2240 – 2253, (2005).

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